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Vol. 19, No. 4, pp. 319-360, 10 figs.

January 18, 1971

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Editors of this number:

Frank B. Cross, Philip S. Humphrey, William E. Duellman

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UNIVERSITY OF KANSAS

Lawrence, Kansas

PRINTED BY

THE UNIVERSITY OF KANSAS PRINTING SERVICE

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INTRODUCTION

Frogs of several families have independently evolved basically similar structures to equip them for arboreal life. Expanded, terminal, digital discs occur in all tree frogs, and it is evident that there has been considerable convergence of evolution of such adaptive features. The employment of only external morphological features to characterize most genera within the Hylidae has resulted in an indeterminate number of constituent genera with obscure phylogenetic relationships.

The genus *Hyla* contains the largest number of species; estimates range as high as 350 (Smith and Taylor, 1948). The genus has become a repository for species that by reason of their apparent lack of morphological or biological specializations cannot readily be referred to other genera. Thus, at this time, any attempt to reconstruct an evolutionary tree of hylids would reveal *Hyla* to be an abnormal branch urgently in need of pruning.

Although the geographic distribution of *Hyla* is disjunct, Pope (1931) and Duellman (1967) have demonstrated the existence of marked external morphological and karyotypic similarities among some of the Nearctic, Oriental and Palaearctic species. The Australian species, in contrast, exhibit extreme morphological divergence, and the majority do not fundamentally resemble species from other geographic regions. In fact, when the Australian species are identified by means of the key to hylid genera prepared by Goin (1961), they key out variously to *Acris*, *Aplastodiscus*, *Pseudacris* and *Hyla*. Martin and Watson (in manuscript) observed similar divergence in larval morphology. In the absence of detailed comparisons of internal anatomy between adequate numbers of Australian species of *Hyla* and those occurring in other geographic regions, it would appear that the generic disposition of the Australian species is assumed rather than demonstrated.

The specificity of mating calls in *Hyla* and their effectiveness as pre-mating isolating mechanisms are well established. However, interspecific variation in form, position and size of the inflated vocal sac has not received comparable attention. Therefore, I undertook a detailed comparison of the sacs, particularly of the superficial

ventral mandibular muscles that form the outer walls of the vocal sac. Because superficial mandibular muscles rarely have been used as taxonomic criteria, it became necessary to survey these structures in other anuran genera. This permitted an evaluation of their phylogenetic significance in the Hylidae and a reasonable interpretation of the taxonomic significance of the observed variation within the genus *Hyla*.

MATERIALS, METHODS AND TERMINOLOGY

The adults and larvae of the hylid genera, species and subspecies examined are listed in the appendix. Dissections were performed with the aid of a low-power binocular microscope, and serial sections were employed in order to clarify the insertions and orientation of muscle fibers in some small species.

There is a lack of uniformity in the nomenclature of the superficial muscles; I have adopted the nomenclature of Kesteven (1944). The names and principal synonyms are: *Musculus submentalis* = *M. intermandibularis anterior* of Trewavas (1933); *Musculus intermandibularis* = *M. intermandibularis posterior* of Trewavas (1933) and *M. submaxillaris* of Beddard (1908) and Duellman (1956, et seq.); *Musculus interhyoideus* = *M. subhyoideus* of Beddard (1908) and Inger and Greenberg (1956) and *M. mylohyoideus* of Liu (1935) and Starrett (1968).

Pectoral muscle nomenclature is that of Jones (1933), and adductor jaw musculature that of Starrett (1968). The larval staging tables of Gosner (1960) were employed in studies of mandibular muscle development.

The systematic arrangement of hylid genera follows Duellman (1970).

SUPERFICIAL MANDIBULAR MUSCULATURE AND VOCAL SAC STRUCTURE IN THE ANURA

To provide a basis for the following comparative morphological data it is necessary first to describe the superficial mandibular musculature and vocal sac structure in anurans. Then problems associated with the current practice of categorizing vocal sac structure will be discussed.

In males and females three separate, superficial, ventral and transversely directed muscles lie between the mandibles (Fig. 1). The first, *M. submentalis*, is an ovoid muscle arising from the lateral, lingual surface of the mandible on each side of the mandibular symphysis. The muscle fibers either traverse from one mandible to the other (Fig. 2a) or meet at a median raphe (Fig. 2b). The sub-

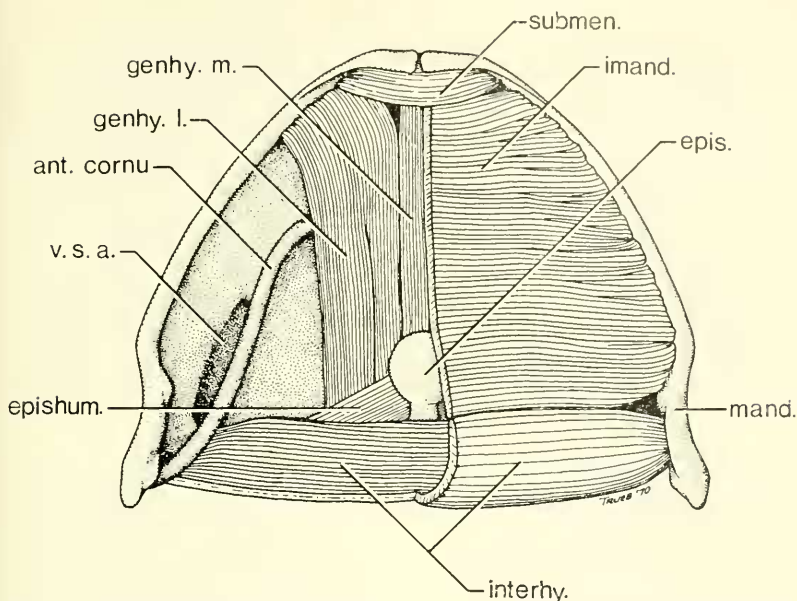


FIG. 1. Intermandibular musculature of a generalized hylid frog. Superficial muscles removed from right side to show deeper musculature. Abbreviations: *ant. cornu*, anterior cornu of hyoid; *epis.*, episternum; *epishum.*, *Musculus* episternohumeralis; *genhy. l.*, *M. geniohyoideus lateralis*; *genhy. m.*, *M. geniohyoideus medialis*; *imand.*, principal element of *M. intermandibularis*; *interhy.*, *M. interhyoideus*; *mand.*, mandible; *submen.*, *M. submental*; *v.s.a.*, vocal sac aperture.

mentalis is capable of limited rotation, provides structural support to the mandibles, and permits limited independent movement of each half of the lower jaw. This muscle is largest in those anurans in which the anterior margin of the lower jaw is truncate; it is smallest in those anurans in which the anterior margin is acuminate or in species in which the mandibles have a bony reinforcement at the symphysis.

The second, *M. intermandibularis*, is a thin, flat sheet of muscle which arises from the lateral, lingual surface of the mandible. The site of origin usually extends along the mandible from the submental anteriorly to the jaw articulation posteriorly. Various relationships of the intermandibularis to the *M. geniohyoideus* need mention here. The *M. geniohyoideus* usually arises from the lingual surface of the mandible. Commonly its origin lies immediately dorsal to the anterolateral portion of the intermandibularis. However, the *geniohyoideus* occasionally arises from a more ventral position; thus, its origin is either partially or totally exposed oc-

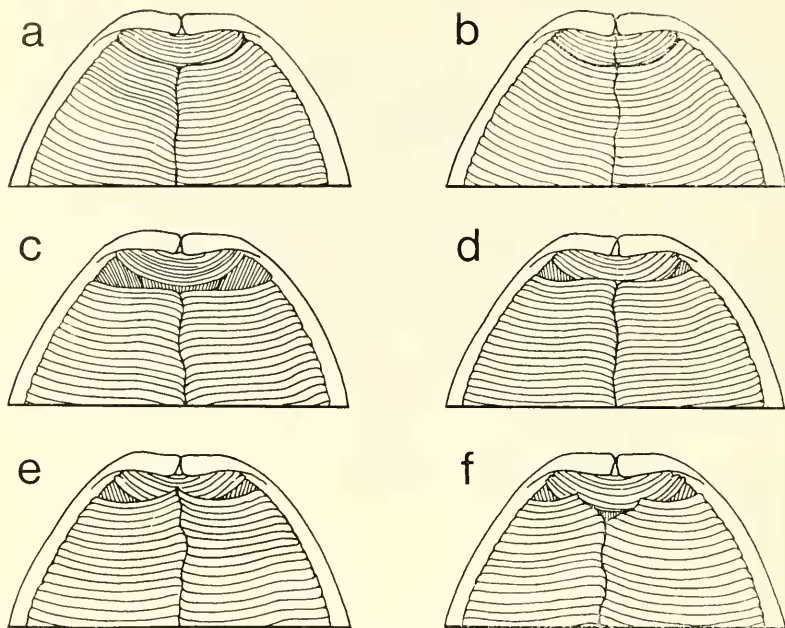


FIG. 2. Variation of anterior intermandibularis musculature in hyloid frogs: (a) araphic submentalis; (b) raphic submentalis; (c) intermandibularis arrested anteriorly; (d) intermandibularis overlaps posterior margin of submentalis; (e) intermandibularis attaches on submentalis posteromedially; (f) intermandibularis attaches on submentalis posterolaterally.

cupying a portion of the mandible and anterior development of the intermandibularis is arrested (Fig. 2c).

The fibers of the two portions of the intermandibularis either meet at the midline along a narrow raphe (Fig. 3a) or they are separated by a median aponeurosis. The aponeuroses vary in shape (Figs. 3b-d).

There is variation in the morphological relationships of the submentalis and intermandibularis. Frequently the muscles lie adjacent to one another (Fig. 2a) or they are partially separated by the geniohyoideus laterally (Fig. 2c). Alternatively the intermandibularis overlaps the posterior margin of the submentalis (Fig. 2d), attaches upon the submentalis posteromedially (Fig. 2e) or posterolaterally (Fig. 2f).

One of the most important forms of variation of the morphology of mandibular musculature is the differentiation of the intermandibularis to form supplementary elements which lie ventral to the usual sheet of the intermandibularis. Hereafter the larger part of

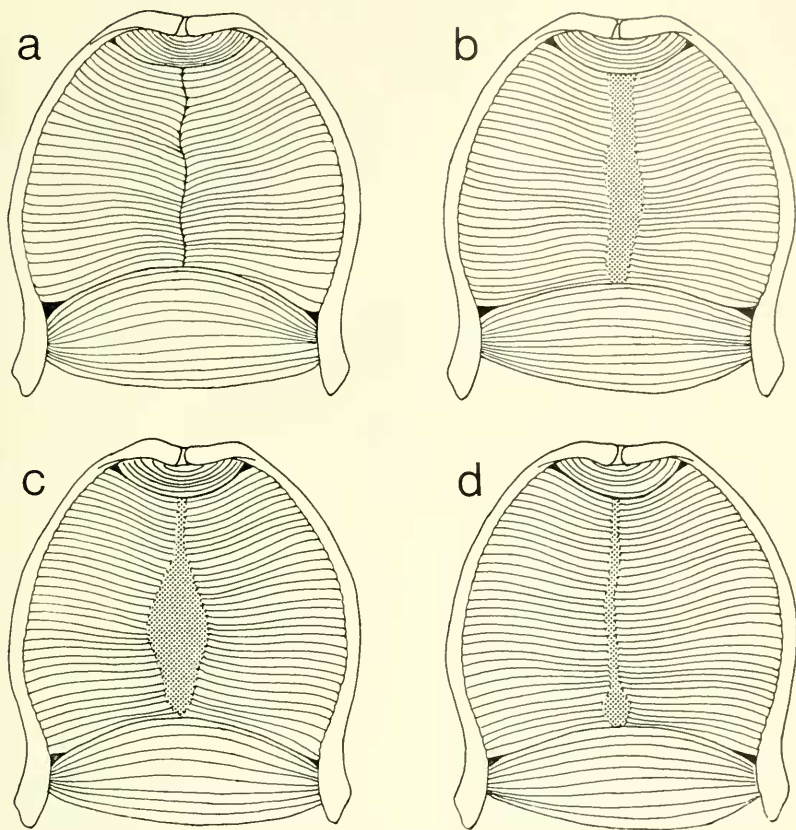


FIG. 3. Medial relationships of intermandibular elements: (a) simple raphe; (b-d) variation in shape of median aponeuroses. Aponeuroses represented by stippled patterns.

the intermandibularis which gives rise to the supplementary elements will be referred to as the "principal element" of the muscle. The supplementary elements are thin, pinnate muscles of such a wide variety of forms (*vide* Trewavas, 1933) that it is difficult to propose a simple classification of their structures. Those supplementary elements which occur in the genera currently referred to the Hylidae vary widely in the position of their origin on the mandibles; they are named accordingly as follows (Table 1):

(1) Apical element—arising from the lingual surface of the mandible on each side of the submentalis. The fibers pass postero-medially and attach upon the median raphe of the principal element (Fig. 4a).

TABLE 1.—Occurrence and kind of Differentiation of the M. Intermandibularis in the Hylidae.

| Genus | Geographic Region | Differentiation | | Kind of supplementary element |
|------------------------|-------------------|-----------------------|----------------------|-------------------------------|
| | | Present (No. species) | Absent (No. species) | |
| <i>Hyla</i> | Australian | 49 | 0 | apical |
| <i>Hyla</i> | Nearctic | 0 | 7 | |
| <i>Hyla</i> | Palearctic | 0 | 1 | |
| <i>Hyla</i> | Oriental | 0 | 2 | |
| <i>Hyla</i> | Neotropical | 3 | 78 | apical |
| <i>Acris</i> | Nearctic | 2 | 0 | apical |
| <i>Agalychnis</i> | Neotropical | 2 | 0 | posterolateral |
| <i>Allophryne</i> | Neotropical | 1 | 0 | anterolateral |
| <i>Amphignathodon</i> | Neotropical | 0 | 1 | |
| <i>Anothecca</i> | Neotropical | 0 | 1 | |
| <i>Aparasphenodon</i> | Neotropical | 0 | 1 | |
| <i>Aplastodiscus</i> | Neotropical | 0 | 1 | |
| <i>Argenteohyla</i> | Neotropical | 0 | 1 | |
| <i>Corythomantis</i> | Neotropical | 0 | 1 | |
| <i>Cryptobatrachus</i> | Neotropical | 0 | 1 | |
| <i>Flectonotus</i> | Neotropical | 0 | 1 | |
| <i>Fritziana</i> | Neotropical | 0 | 2 | |
| <i>Gastrotheca</i> | Neotropical | 0 | 3 | |
| <i>Hemiphractus</i> | Neotropical | 0 | 2 | |
| <i>Limnaoedus</i> | Nearctic | 0 | 1 | |
| <i>Nyctimantis</i> | Neotropical | 0 | 1 | |
| <i>Nyctimystes</i> | Australian | 9 | 0 | apical |
| <i>Osteocephalus</i> | Neotropical | 0 | 5 | |
| <i>Pachymedusa</i> | Neotropical | 1 | 0 | posterolateral |
| <i>Phrynohyas</i> | Neotropical | 0 | 3 | |
| <i>Phyllodytes</i> | Neotropical | 0 | 1 | |
| <i>Phyllomedusa</i> | Neotropical | 9 | 0 | posterolateral |
| <i>Plectrohyla</i> | Neotropical | 0 | 2 | |
| <i>Pseudacris</i> | Nearctic | 0 | 3 | |
| <i>Pternohyla</i> | Neotropical | 0 | 1 | |
| <i>Ptychohyla</i> | Neotropical | 0 | 2 | |
| <i>Smilisca</i> | Neotropical | 0 | 3 | |
| <i>Sphaenorhynchus</i> | Neotropical | 3 | 0 | apical |
| <i>Trachycephalus</i> | Neotropical | 0 | 2 | |
| <i>Triprion</i> | Neotropical | 0 | 2 | |

(2) Anterolateral element—arising from the lingual surface of the mandible on the anterior portion of the bone. The fibers pass anteriorly, parallel to the mandible, and attach upon the ventral surface of the submentalis (Fig. 4b).

(3) Posterolateral element—arising from the ventral surface of the mandible near the site of mandibular articulation. The fibers pass

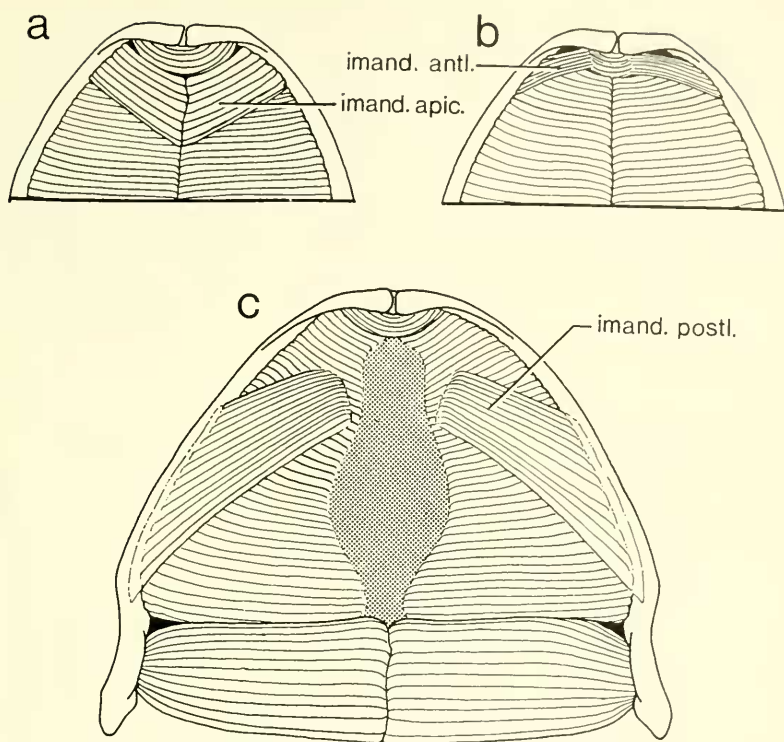


FIG. 4. Supplementary intermandibular elements of the Hylidae: (a) apical element; (b) anterolateral element; (c) posterolateral element. Abbreviations: *imand. antl.*, anterolateral element of M. intermandibularis; *imand. apic.*, apical element of M. intermandibularis; *imand. postl.*, posterolateral element of M. intermandibularis.

anteromedially and attach upon the ventral surfaces of the principal element (Fig. 4c).

The third major superficial muscle, the interhyoideus, usually arises from the anterior cornu of the hyoid near its termination on the skull at the crista parotica. The muscle accompanies the anterior cornu along its ventral path to the region of the post-articular portion of the mandible. From the articular region, the anterior cornu passes anteriorly along the lingual surface of the mandible, whereas the interhyoideus fibers diverge medially and form a transverse sheet (Fig. 1). Anteriorly this sheet unites with the posterior border of the intermandibularis; posteriorly it is connected to the M. episternohumeralis by a broad sheet of collagenous connective tissue.

There is considerable variation in the size and form of the in-

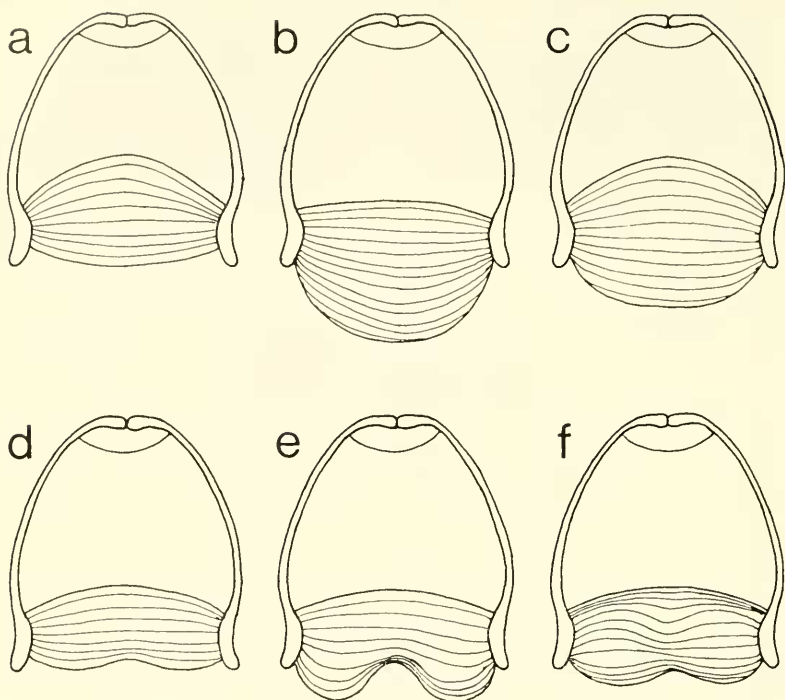


FIG. 5. Variation in development of interhyoideus in the Hylidae: (a) anterior development; (b) posterior development; (c) anterior and posterior development; (d) slight bilobular posterior development; (e) posterolateral bilobular development; (f) ventral bilobular development.

terhyoideus. This morphological diversity is associated with the development of the vocal sac apparatus. Within the Hylidae, the most frequently encountered forms of the interhyoideus are as follows:

- (1) Remains in the form of a transverse sheet of parallel fibers (Fig. 1).
- (2) Anterior development accompanied by reduction of the posterior extent of the intermandibularis, particularly medially (Fig. 5a).
- (3) Posterior development which results in a single lobe lying upon the sternal musculature (Fig. 5b).
- (4) Anterior and posterior development (combination of conditions 3 and 4—Fig. 5c).
- (5) Slight posterolateral, bilobular development (Fig. 5d).
- (6) Extreme posterolateral bilobular development (Fig. 5e).
- (7) Ventral bilobular development (Fig. 5f).

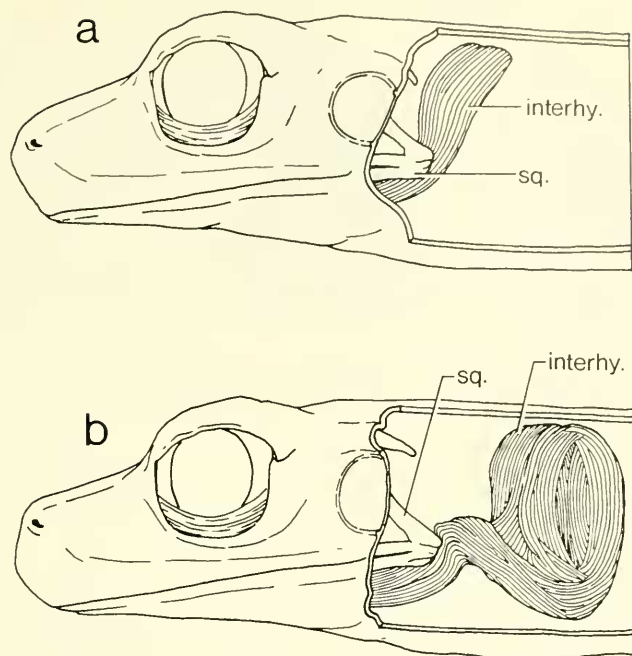


FIG. 6. Supramandibular lobes of interhyoides: (a) tubular extension; (b) convoluted pouch. Abbreviations: *interhy.*, M. interhyoides; *sq.*, squamosal.

(8) Supramandibular development involving the development of a slender, tubular extension (Fig. 6a).

(9) Supramandibular development involving the development of a broad, convoluted, tubular extension (Fig. 6b).

Anuran vocal sacs are customarily described as being diverticula of the lining of the mouth, and communicating with the mouth by paired or single, round or slit-like apertures. A vocal sac actually represents an extrusion of a portion of the lining of the mouth into a site directly above the superficial, ventral mandibular muscles. The lining of the mouth consists of a dense layer of collagenous connective tissue upon which there is a superficial layer of pseudo-stratified, columnar epithelium, most of which is ciliated. The mouth is completely underlain by muscles except for small areas bordered by the mandible laterally, the geniohyoideus lateralis medially. Consequently the lining of the mouth is free to extrude ventrally between these muscles and the ventral, superficial muscle block only in these lateral areas. In some species the extrusions, which represent the vocal sac, form a single cavity into which both

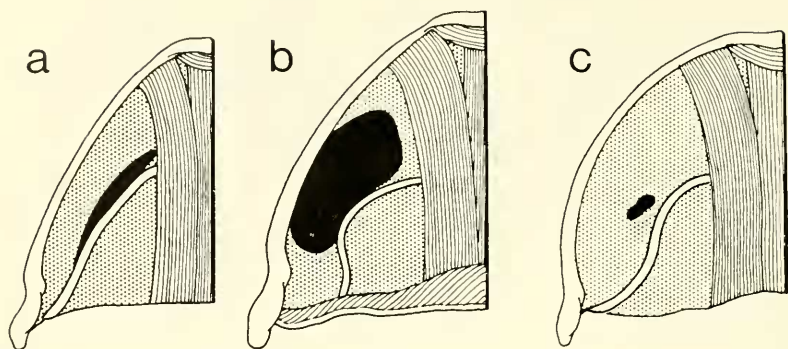


FIG. 7. Vocal sac apertures of hyliids: (a) slit; (b) gaping hole; (c) small orifice.

vocal apertures open. In other species the extrusions or cavities remain separate, each associated with its own aperture, to form two discrete vocal sacs. This "unsupported" area between the lining of the mouth and the ventral superficial muscles is traversed by the anterior cornu of the hyoid which invariably forms the medial margin of the aperture. The apertures are in the form of slits (Fig. 7a), gaping holes (Fig. 7b) or small orifices in the floor of the mouth (Fig. 7c).

Tyler (1970) reviewed and illustrated various submandibular myo-integumental relationships and the ways in which these may influence the evolution of the vocal sac apparatus. Such relationships reported here are 1) the relative development of the post-mandibular septum described as short, moderate or deep; 2) The presence or absence of post-septal development of the interhyoideus, and 3) the presence or absence of direct contact of intermandibular muscles with the skin.

The innervation of the superficial mandibular muscles and of the skin adjacent to the muscles is as follows: the submentalis and intermandibularis are innervated by the fifth cranial (trigeminal) nerve, and the interhyoideus by the seventh cranial (facial) nerve.

The presence of superior or posterolateral extensions of the interhyoideus associated with the vocal sac has been recorded in several genera by Liu (1935). Such sacs are usually described as being paired, "lateral," or "posterolateral" in contrast to the more common single, median, "subgular" structure. The other major classification of vocal sacs involves the distinction of their being "internal" or "external." Noble (1931) defined these latter categories as follows: "When the skin is so modified that it balloons

out into a pair of such sacs one on each side of the throat, the sacs are said to be 'external.' But if the skin of the throat is not thinned, the whole throat merely assuming a swollen appearance when the frog calls, the sacs are said to be 'internal'."

Skin "modification" includes (1) the presence of discrete, inverted or everted dermal lobes to receive the underlying muscle when the sac is inflated, (2) extensive irregular pleating or folding of the skin over the entire submandibular region, or (3) the presence of single transverse pre- or post-axillary folds. It is evident that the present terminology results in the allocation of totally dissimilar structures to the same category, thus masking the existence of morphological variation. Accordingly, wherever possible, I have substituted names that indicate the position of the major portion of the vocal sac in relation to the mandibles or anterior segment of the sternum.

COMPARATIVE MORPHOLOGY

Phyllomedusinae

Agalychnis, *Pachymedusa*, and *Phyllomedusa* have similar superficial mandibular musculature. The submentalis is small, araphic and completely visible from the ventral aspect, there being no muscular attachments of the intermandibularis on it. The intermandibularis is differentiated to produce supplementary posterolateral elements (Fig. 4c). Each posterolateral element arises from the ventral surface of the mandible and is attached by a broad ligament to one of two adductor muscles of the jaw. (Starrett, 1968, reported variation in the nature of the adductor musculature of *Phyllomedusa*.) In species in which the M. adductor mandibulae posterior subexternus is present, the ligament attaches to it; the site of attachment is covered by the M. a.m. externus superficialis. In those species lacking the former muscle, the ligament attaches directly to the latter. The posterolateral element of the intermandibularis passes anteromedially from its site of origin and attaches to the principal muscle lateral to a broad, median aponeurosis. The aponeurotic portion of the intermandibularis adheres dorsally to the geniohyoideus.

The interhyoideus is well developed, lacks folds and pleats, and shows no evidence towards bilobular development in any of the species examined. A vocal sac is present in all species except *Phyllomedusa edentula*. The sac lies above the interhyoideus, extending anterolaterally dorsal to the intermandibularis. The vocal sac apertures are customarily short slits, equivalent in length to approxi-

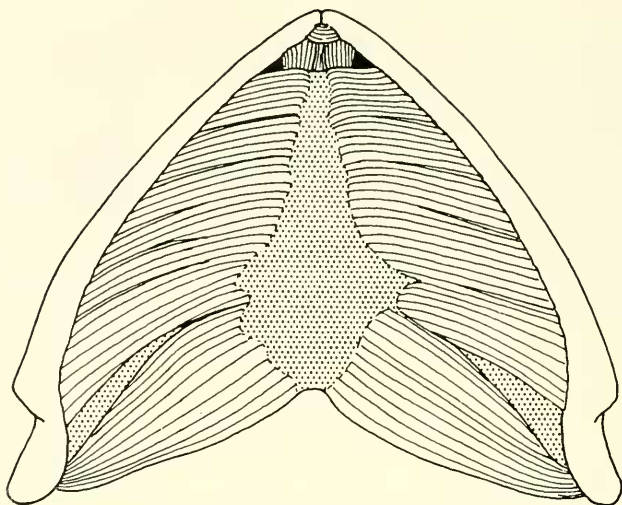


FIG. 8. Intermandibular musculature of *Hemiphractus*. Median and posterolateral aponeuroses represented by stippled patterns.

mately one-tenth the length of the mandible; they are located dorsal to the site of origin of the posterolateral elements of the intermandibularis.

There is no direct myointegumental contact. The postmandibular septum is of moderate length and attached to the posterior end of the interhyoideus.

Hemiphractinae

The submentalis of *Hemiphractus* is extremely small and agraphic (Fig. 8). The intermandibularis is not differentiated and is poorly developed. It is characterized by incomplete anterior development, which results in a broad gap between the submentalis and intermandibularis. The intermandibularis bears a vast, median aponeurosis through which the geniohyoidei are clearly visible. The muscle fibers are exceptionally thin.

The interhyoideus, like the intermandibularis, is poorly developed. It is separated from the intermandibularis by an aponeurosis. The median portion of the muscle is aponeurotic.

The single species examined lacks a vocal sac. There is no direct myointegumental contact. The post-mandibular septum is short and attached to the posterior end of the interhyoideus.

Amphignathodontinae

The only specimen of the rare, monotypic genus *Amphignathodon* available for study is a female. The submentalis is of moderate size, completely visible, and bears a median raphe. The intermandibularis is not differentiated, and bears an aponeurosis in the form of an elongated diamond. The interhyoideus is of moderate size and is aponeurotic anteromedially.

There is no direct myointegumental contact. The postmandibular septum is short and attached to the posterior end of the interhyoideus.

The submentalis of *Anothea* is of moderate size and araphic. The intermandibularis is not differentiated; there is anteromedial attachment of the fibers upon the posterior margin of the submentalis. The anterior half of the fibers of the remainder of the muscle meet at a median raphe; the posterior half of the muscle bears a broad median aponeurosis. This aponeurosis extends posteriorly into the interhyoideus. *Anothea spinosa* lacks a vocal sac, and there is no direct myointegumental contact. The postmandibular septum is moderate and attached to the posterior end of the interhyoideus.

The submentalis of *Cryptobatrachus* is of moderate size and araphic. The intermandibularis is not differentiated and lacks an aponeurosis. The most anterior fibers of the intermandibularis attach anteromedially upon the posterior margin of the submentalis. The interhyoideus is not developed anteriorly or posteriorly. There is no vocal sac and no direct myointegumental contact. The postmandibular septum is deep and attached to the posterior end of the interhyoideus.

Among hylid genera, *Flectonotus* is uniquely characterized by the broad overlap of the anterior part of the intermandibularis on the moderate sized, araphic submentalis. The intermandibularis is not differentiated; the anterior half of the muscle bears a median raphe and the posterior half bears a small median aponeurosis. The interhyoideus is not developed anteriorly or posteriorly. The vocal sac is large, extending anteriorly almost to the level of the submentalis. The apertures are large gaping holes slightly more than one-third the length of the mandible. There is no direct myointegumental contact. The postmandibular septum is short and attached to the posterior end of the interhyoideus.

The submentalis of *Fritziana* is small, araphic and rather elongate. The intermandibularis is not differentiated; the anterior-most

fibers attach upon the posteromedial border of the submentalis. This muscle bears a median raphe and lacks an aponeurosis. The interhyoideus is not developed anteriorly or posteriorly. The vocal sac extends anteriorly to the mid-level of the intermandibularis. The vocal sac apertures are gaping holes, one-third the length of the mandible; their posterior margins are located at the level of the posterolateral limit of the intermandibularis. The aperture is bordered posteromedially by the anterior cornu of the hyoid and anteromedially by the geniohyoideus laterali. There is no direct myointegumental attachment. The postmandibular septum is moderate and attached to the posterior end of the interhyoideus.

In *Gastrotheca* the submentalis is small, araphic and completely visible. The intermandibularis is not differentiated, and there is no muscular contact between the anterior fibers and the submentalis. The intermandibularis bears a median raphe and lacks a median aponeurosis. The interhyoideus exhibits considerable anteromedial development; it bears a large, median lobe which displaces the intermandibularis in this area. A vocal sac is present in *marsupiatum* and *nicefori* but absent in *ceratophrys*. In the first species it extends midway above the intermandibularis. The vocal sac apertures are holes equivalent in length to one-fifth of the length of the mandible. In the specimen of *marsupiatum* a few medial fibers located midway along the interhyoideus attach directly to the underlying skin. The area of contact measures approximately 2 mm. \times 1 mm. The postmandibular septum is deep and a portion of the interhyoideus extends posterior to it.

The submentalis of *Nyctimantis* is of moderate size, araphic and obscured by dense, opaque, fibrous tissue. The intermandibularis is not differentiated; the anterior fibers attach upon the posterolateral margin of the submentalis. The intermandibularis bears an elongate, median aponeurosis which does not adhere to the muscles above it. The interhyoideus is a large muscle developed both anteriorly at the expense of the intermandibularis, and posteriorly beyond the postarticular extremities of the mandibles. The vocal sac extends anteriorly about midway along the intermandibularis beneath the aponeurosis. The vocal sac apertures are holes located near the lateral margin of intermandibularis and interhyoideus; their length is equivalent to one-sixth of the length of the mandible. There is no direct myointegumental contact. The postmandibular septum is moderate and attached to the posterior border of the interhyoideus.

Hylinae

Acris exhibits an araphic submentalis of small size. The intermandibularis is differentiated and the supplementary elements are of the apical type. The position of the apical element is identical to that of *Nyctimystes* but it is an extremely thin sheet and cannot be freely separated from the principal muscle. The principal element of the intermandibularis lacks an aponeurosis, the interhyoideus is very well developed anteriorly. The vocal sac extends anteromedially beneath the posterior one-third of the intermandibularis. The vocal sac apertures are slits equivalent in length to approximately one-quarter of the length of the mandible. There is no direct myointegumental contact. The postmandibular septum is moderate and there is slight development of the interhyoideus posterior to it.

The submentalis of *Allophryne* is elongate and araphic. The intermandibularis is differentiated and the supplementary elements are of the anterolateral type. These attach upon the ventral surface of the submentalis (Fig. 4b). The intermandibularis lacks a median aponeurosis. The only specimen available for study is a partially dissected female and no further data were obtainable.

Aparasphenodon is characterized by a small, araphic submentalis and an undifferentiated intermandibularis bearing an elongate, median aponeurosis which is broadest at its posterior limit. The interhyoideus is not well developed anteriorly or posteriorly, but is folded and pleated ventrally, particularly near the mandible. The vocal sac is a paired submandibular structure, medial adhesions preventing communication between the two portions. Anterolaterally the sacs extend as far as the middle of the intermandibularis. The vocal sac apertures are elongate holes situated on the lateral margin of the mandible and equivalent to approximately one quarter of its length. There is no direct myointegumental attachment. The postmandibular septum is short and attached to the posterior end of the interhyoideus.

In *Aplastodiscus* the submentalis is small and araphic. The intermandibularis is not differentiated and lacks an aponeurosis. Anteriorly the fibers of the intermandibularis attach upon the posteromedial border of the submentalis. The interhyoideus is not well developed anteriorly or posteriorly. The vocal sac extends anteriorly almost as far as the submentalis. Vocal sac apertures are short slits located approximately midway along the length of the mandible. Their length is less than one sixth of the length of the mandible. There is no direct myointegumental contact. The position and

development of the postmandibular septum could not be detected as a result of dehydration.

Argenteohyla has a small araphic submentalis. The intermandibularis is not differentiated; its most anterior fibers attach upon the posterolateral border of the submentalis. The interhyoideus is not well developed anteriorly or posteriorly. There is no direct myointegumental attachment. The postmandibular septum is short, attaching to the posterior border of the interhyoideus. A male has not been examined but Barrio (1966) provided a photograph of one with the vocal sac inflated. This depicts a bibobular postmandibular structure.

The submentalis of *Corythomantis* is small and araphic. The intermandibularis is not differentiated, lacks any form of attachment to the submentalis, and lacks an aponeurosis. The interhyoideus lacks anterior and posterior development but ventrally is folded and pleated, particularly near the mandibles. The vocal sac is separated into two parts as a result of extensive median adhesions between the interhyoideus and the muscles dorsal to it. The vocal sac apertures are situated at the anterior limit of the vocal sac. They are gaping holes, their length equivalent to approximately one-fifth of the length of the mandible. There is no direct myointegumental contact. The postmandibular septum is short, attaching to the posterior end of the interhyoideus.

The species of *Hyla* are here divided according to their geographic distribution:

(1) *Australia and New Guinea (Australo-Papuan).*—The intermandibularis is differentiated by the development of a supplementary apical element (Fig. 4a). Attachments of the anterior fibers of the principal muscle of the intermandibularis to the medial border of the submentalis occur in only two of the 49 species examined: *nasuta* and *nigrofrenata*. In no species is there a broad lateral gap between the submentalis and intermandibularis; the interhyoideus is well developed anteriorly.

The absence of a vocal sac reported in *H. lesueuri* by Duméril and Bibron (1841) and *H. eucnemis* by Liu (1935) has been confirmed; a similar condition has been found in *H. booroolongensis* and *H. genimaculata*. In all other species a vocal sac is present and is usually substernal and unilobular. Anteromedially the vocal sac does not extend beyond a position above the posterior apex of the apical element of the intermandibularis.

In some individuals of *H. infrafronata*, the largest member of the genus, the vocal sac is a submandibular, bilobular structure whereas

in others it is unilobular. The form of the structure is apparently determined by the position of the episternum which in this species involves a secondary sexual modification that Boulenger (1912) considered unique in the Hylidae. The episternum of female *infra-frenata* is cartilaginous and terminates in the customary flattened disc lying dorsal to the interhyoideus. In adult males it is entirely ossified and consists of a broad process tapering to a sharp spike. The omosternum either lies ventral to the interhyoideus or projects into its posterior folds. In the former case the skin surrounding the episternum forms a separate sheath producing a bilobular sac, whereas it forms a unilobular sac in the latter. Where the episternum lies ventral to the interhyoideus the position of the tip of the spike is visible externally as a sharp projection.

Vocal sac apertures in Australo-Papuan species are slits or gaping holes, their length one quarter to one half of the length of the mandible. There is no direct myointegumental contact. The post-mandibular septum is of moderate length.

(2) *Nearctic, Palaearctic and Oriental species*.—These species differ from the Australo-Papuan in having an intermandibularis which is not differentiated. They are also characterized by transverse overlap of the anterior fibers of the intermandibularis upon the submentalis, an intermandibularis lacking an aponeurosis, anterior and posterior development of the interhyoideus, and a large, unilobular, submandibular vocal sac. Vocal sac apertures are in the form of slits or holes; their length varies from one quarter to one half of the length of the mandible. There is variation in the development of the postmandibular septum, the presence or absence of development of the interhyoideus posterior to it, and in the existence of myointegumental contact.

(3a) *Neotropical species (West Indies)*.—The nine West Indian species represent at least three separate phyletic lines (*vide* Duellman, 1970), one of which is represented by the *H. septentrionalis* group comprising *septentrionalis*, *dominicensis* and *brunnea*. In this species group the intermandibularis is differentiated by the development of an apical element. This apical element differs from that exhibited by Australian *Hyla* and *Nyctimystes* in that the muscle fibers attach to the principal muscle over an extensive area whereas in the former representatives attachment occurs only at the median raphe. Attachments of the anterior fibers of the principal muscle to the submentalis are anteromedial. The interhyoideus is well developed anteriorly and posteriorly, the latter margin being unilobular in *brunnea* and slightly bilobular in *dominicensis* and *sep-*

tentrionalis. The size of the vocal sac aperture is correlated with this divergence. In *brunnea* the vocal sac extends anteromedially to a position above the apex of the apical element, and the apertures are slits one third as long as the mandible. In the other two species the vocal sac is confined to the interhyoideus and the vocal sac apertures are small orifices one tenth the length of the mandible. There is no direct myointegumental contact. The postmandibular septum attaches to the posterior end of the interhyoideus.

None of the remaining species has the intermandibularis differentiated and in all except *pulchrilineata* this muscle bears an elongate, median aponeurosis. The same species is distinguished from all other West Indian species by its possession of supramandibular lobes to the interhyoideus lying upon the dorsal fasciae posterior to the depressor mandibulae. *Hyla heilprini* is the only species having a dermal, submental gland, and *marianae* is unique (among West Indian hylids) in lacking a vocal sac.

Hyla lichenata and *vasta* exhibit slight bilobular ventrolateral development of the interhyoideus and also share with *dominicensis* and *septentrionalis* apertures in the form of small orifices, equivalent in length to one tenth of the length of the mandible.

(3b) *Neotropical species (Central and South America)*.—These species exhibit considerable morphological variation; the present account is confined to a description of the range of variation observed pending an anticipated computer analysis of species groups combining myological, osteological and biological data.

In all species examined the submentalis is araphic and the intermandibularis is not differentiated; attachments of the intermandibularis upon the submentalis are present or absent and the intermandibularis exhibits or lacks a median aponeurosis.

There is considerable diversity in the development of the interhyoideus and vocal sac. The following species have submandibular, bilobular extensions of the interhyoideus: *brieni*, *catharinae*, *colymba*, *crospedospila*, *depressiceps*, *garbei*, *hayi*, *nasica*, *phrynoderma*, *pickeli*, *smaragdina* and *subocularis*. Their interhyoideal pouches are not uniform. In *hayi* there is simply a slightly bilobular border to the muscle; at the other extreme (*smaragdina*) the separation is distinctive. *Hyla marmorata* possesses a vast, unilobular, posterior interhyoideal lobe extending far beyond the postarticular portions of the mandibles. Although there is no myological evidence for the existence of a bilobular structure when the vocal sac is inflated, the skin covering the forearm to the elbow is greatly distended away from the muscle. Additionally the position of the pec-

toral lymphatic septum is modified in a way that permits the inflated sac to intrude into these subhumeral spaces.

Hyla alboguttata and *punctata* are the only species in which there is evidence for the development of the interhyoideus dorsally. In the former species thin-walled supramandibular labes reach the level of the tympanum. In *punctata* I was unable to find a dilatable lobe; the most posterior fibers simply overlie the postarticular portion of the mandible; a few fibers attach to the skin. *Hyla penhether* and *robertsorum* lack vocal sacs.

Vocal sac apertures are situated more posteriorly and are shorter in species having bilobular vocal sacs than in those having unilobular sacs.

In many species the skin covering the submandibular region is greatly convoluted, extremely thin, unpigmented and partially transparent. In *rhodopepla* both the skin covering the superficial muscles and the muscles themselves are so thin that the deeper musculature and associated structures are visible externally. A large, submental dermal gland occurs in *colymba*; a less well developed structure is present in some individuals of *rivularis* but is absent in others.

Extensive, direct myointegumental contact involving the interhyoideus occurs in many small species.

The submentalis of *Limnaeodius* is of moderate size and araphic. The intermandibularis is not differentiated; the most anterior fibers attach upon the posterolateral border of the submentalis. The intermandibularis lacks an aponeurosis. The interhyoideus is very well developed anteriorly and posteriorly. The vocal sac is a vast structure extending anteriorly to a position midway above the intermandibularis. The vocal sac apertures are holes, their length equivalent to one-quarter of the length of the mandible. There is no direct myointegumental contact. The postmandibular septum is short; there is a small portion of the interhyoideus posterior to the site of attachment.

The submentalis of *Nyctimystes* is of moderate size, araphic and completely visible from the ventral aspect. The intermandibularis is differentiated and the supplementary elements are of the apical type (Fig. 4a). The principal muscle lacks attachment to the submentalis and bears a median raphe. It extends anteriorly to the submentalis in all species. The interhyoideus is well developed anteriorly.

Absence of vocal sac has been reported previously to characterize *N. papua* (Parker, 1936) and *N. avocalis* (Zweifel, 1958). It is also absent in *N. tympanocryptis*. The vocal sac of *Nyctimystes*

extends anteromedially to a position above the posterior limit of the apical element of the intermandibularis, and anterolaterally to a position midway between the submentalis and interhyoideus. Vocal sac apertures are slits, one-quarter to one-third as long as the mandible; their posterior margins lie beneath the posterolateral junction of intermandibularis and interhyoideus. There is no direct myointegumental contact. The postmandibular septum is of moderate length and is attached to the posterior end of the interhyoideus.

In all species of *Osteocephalus* the submentalis is of moderate size and araphic, and the intermandibularis is not differentiated. *Osteocephalus buckleyi* lacks any attachment between the anterior fibers of the intermandibularis and the submentalis; there is minimal posterolateral attachment in the other species. All species have an elongate median aponeurosis on the intermandibularis; it is broadest in *buckleyi*. There is considerable variation in the development of the interhyoideus and of the skin covering it, associated with the development of supramandibular vocal sac structures. In *buckleyi*, *lepreuri* and *verrucigerus* there is simply a slender tubular posterolateral extension, passing posterior to the extremity of the mandible and adhering to the dorsal fasciae. In *taurinus* the supramandibular portion of the interhyoideus is much broader, and there is an everted pouch of skin (thinner than that surrounding it) located lateral to it. The skin pouch of *buckleyi* is smaller than that of *taurinus* and is not visibly distinguishable from the skin of the surrounding area; *lepreuri* and *verrucigerus* lack pouches. The supramandibular vocal sacs are not discrete, communication being maintained within the posterior border of the intermandibular portion of the interhyoideus. Vocal sac apertures are small orifices located at the entrances to the interhyoidal extension; their length is approximately one seventh the length of the mandible in those species possessing skin pouches, and one fifteenth in those lacking them. No species has direct myointegumental attachment. The postmandibular septa are short and attached to the posterior end of the intermandibular portion of the interhyoideus.

The superficial mandibular musculature and vocal sac structure of *Phrynohyas* were described in detail by Duellman (1956); they are similar in most respects to those of *Osteocephalus taurinus*. The only supplementary data are that the length of the vocal sac apertures is approximately one-fifth the length of the mandible. There is no direct myointegumental attachment. The postmandibular sep-

tum is short and attached to the posterior end of the intermandibular portion of the interhyoideus.

The submentalis of *Phyllodytes* is elongate and araphic. The intermandibularis is not differentiated and bears a broad median aponeurosis; the most anterior fibers attach upon the posterolateral border of the submentalis. The interhyoideus is well developed anteriorly and extends posteriorly slightly beyond the mandible. The anterior limit of the vocal sac is on a level with a point midway between the submentalis and the interhyoideus. The vocal sac apertures are holes, their lengths equivalent to approximately one-quarter of the length of the mandible. There is no direct myointegumental contact. The postmandibular septum is moderate and attached to the posterior end of the interhyoideus.

Plectrohyla exhibits a small, araphic submentalis; its posterior border is obscured by transverse fibers of the intermandibularis. The intermandibularis is not differentiated and lacks an aponeurosis. The interhyoideus is not developed anteriorly in *guatemalensis*, which lacks a vocal sac, and is slightly developed in *ixil* which possesses one. The vocal sac extends anteromedially to a position slightly anterior to the border of the intermandibularis and interhyoideus. The vocal sac apertures are long slits one-third the length of the mandible. In *ixil* there is extensive direct myointegumental contact involving the posterior half of the interhyoideus, but no contact in *guatemalensis*. The postmandibular septum is extremely short in both species, attaching to the posterior end of the interhyoideus.

The submentalis of *Pseudacris* is small and araphic. The intermandibularis is not differentiated and lacks an aponeurosis; its anterior fibers traverse the posterior margin of the submentalis. The interhyoideus is very well developed anteriorly and slightly posteriorly. The vocal sac extends anteromedially to a position midway between the medial boundary of the intermandibularis and submentalis. The vocal sac apertures are extremely long slits, their length being almost one-half the length of the mandible. There is no direct myointegumental attachment. The postmandibular septum is moderate and there is slight development of the interhyoideus posterior to its site of attachment.

Pternohyla has a small, araphic submentalis. The intermandibularis is not differentiated, lacks an aponeurosis and lacks attachment of fibers to the submentalis. The interhyoideus is developed slightly anteriorly and considerably posteriorly forming a vast lobe extending far beyond the postarticular extremities of the mandibles. The vocal sac extends anteriorly to a position nearer to the submentalis

than to the border of the intermandibularis and interhyoideus. The vocal sac apertures are elongate slits, their length equivalent to one-third of the length of the mandible. There is no direct myointegumental contact. The postmandibular septum is short and there is slight development of the interhyoideus posterior to the site of attachment.

The submentalis of *Ptychohyla* is small and araphic, its posterior border traversed by the most anterior fibers of the intermandibularis. The intermandibularis is not differentiated and bears a median aponeurosis which is narrow anteriorly and broad posteriorly. The interhyoideus is slightly developed anteriorly and posteriorly and bears numerous transverse folds. The vocal sac extends anteriorly to a position just anterior to the border of the intermandibularis and interhyoideus in *leonhardschultzei*, and almost reaches the submentalis in *spinipollex*. The vocal sac apertures are narrow slits approximately one quarter the length of the mandible. There is no direct myointegumental contact. The postmandibular septum is short and attached to the posterior end of the interhyoideus.

The superficial mandibular musculature and vocal sac structure of *Smilisca* were described by Starrett (1960) and Duellman and Trueb (1966). The only supplementary data are that the interhyoideus is developed anteriorly as well as ventrolaterally. The vocal sac apertures are elongate slits terminating anteriorly at the site of attachment of the geniohyoideus lateralis; their length is more than one third of the length of the mandible. There is extensive direct myointegumental contact of the interhyoideus in most specimens. The postmandibular septum is short and attached to the posterior end of the interhyoideus.

In ventral view the mandibular musculature of *Sphaenorhynchus* is so dominated by the vocal sac structure that the appearance is of a vocal sac with a frog attached to it. The submentalis is small and araphic. The intermandibularis is differentiated by a perfectly developed but extremely small apical element (Fig. 9). Consequently, the orientation of the fibers of the apical element is mainly transverse; thus the most anterior fibers of the intermandibularis overlie the submentalis, obscuring its posterior border. The interhyoideus is exceptionally well developed posteriorly, extending considerably beyond the postarticular extremities of the mandibles. The vocal sac extends anteromedially to the anterior limit of the interhyoideus. The vocal sac apertures are slits; their length is slightly less than one third of the length of the mandible. There is extensive direct myointegumental contact of the interhyoideus. The

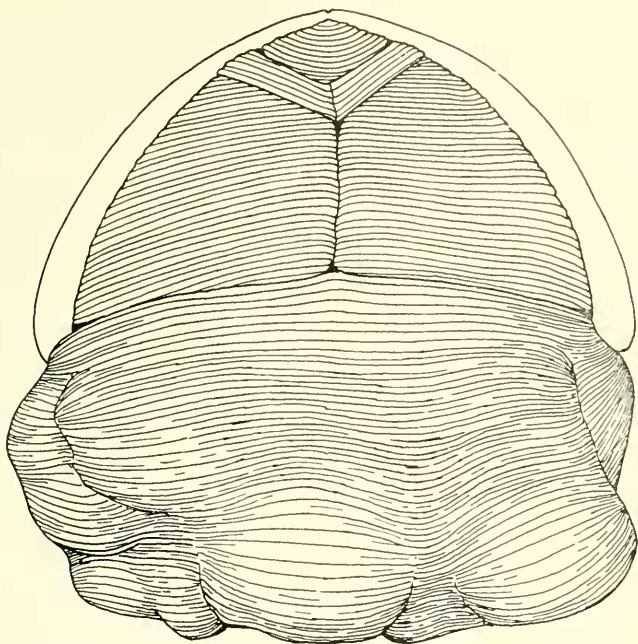


FIG. 9. Intermandibularis musculature of *Sphaenorhynchus*.

postmandibular septum is moderate and there is considerable development of the interhyoideus posterior to its site of attachment.

The submentalis of *Trachycephalus* is of moderate size and agraphic. The intermandibularis is not differentiated and lacks an aponeurosis. The interhyoideus forms vast supramandibular lobes comparable to those occurring in *Phrynohyas*, and the vocal sacs are similar to those in that genus. The vocal sac apertures are holes; their length is less than one quarter of the length of the mandible. There is direct myointegumental contact between the supramandibular lobes of the interhyoideus and the associated skin sac, permitting partial inversion of the latter. The postmandibular septum is moderate and is attached to the posterior border of the intermandibular portion of the interhyoideus.

The superficial mandibular musculature and vocal sac structure of *Triprion petasatus* were described by Duellman and Klaas (1964). The vocal sac structures are paired and submandibular. The discrete shapes of these structures in this species and in *T. s. spatula* are not as apparent in preserved specimens as they are in *Smilisca*. The interhyoideus is exceptionally thin—in sagittal section 0.25 mm. compared with 0.7 mm. for the intermandibularis; thus

the lobes of the muscle are compressed flat when the vocal sac deflates. The vocal sac apertures are slits one seventh the length of the mandible. The position of the apertures is misrepresented in the illustration provided by Duellman and Klaas (1964); they are situated on the mandibular and not the lingual border of the anterior cornua. There is limited myointegumental contact involving the interhyoideus. The postmandibular septum is moderate and attaches to the posterior border of the interhyoideus.

Differentiation of the M. intermandibularis in other Anurans

Because the nature of the intermandibularis has not been employed formerly as a taxonomic criterion, 124 species representing 57 genera in nine anuran families other than Hylidae were examined. Recorded in Table 2 are observations on 32 genera in which either at least two species were dissected, or where data provided by Trewavas (1933) supplement mine. It will be noted that in each genus all species either possess supplementary elements to the intermandibularis, or else all lack them.

DEVELOPMENT OF SUPERFICIAL MANDIBULAR MUSCULATURE

The superficial mandibular muscles develop concomitantly with the mandibles during metamorphic climax. Detailed information on the ontogeny and larval functions of these muscles has been confined hitherto to representatives of genera such as *Bufo* (Sedra, 1950) and *Rana* (de Jongh, 1968), in which the intermandibularis is not differentiated.

Tadpoles of four Australian species of *Hyla* were studied to establish the stage at which the intermandibularis differentiates, thereby permitting an evaluation of the functional significance of differentiation. No specific differences worthy of note were observed and the following account based on a series of *Hyla thesaurensis* is considered typical of Australian species.

Stage 41 immediately precedes the emergence of the forelimbs; the larval mouthparts persist and the mandibular muscles retain the typical larval form (Fig. 10a). At this stage the M. mandibulolabialis arises from the caudal side of the Meckel's cartilage, fans out broadly, and attaches to the ventral margin of the lower lip. There is no submentalis. The intermandibularis consists of a broad loop of fibers arising from the ventral surface of the Meckel's cartilage, while the interhyoideus is a slender band of transversely directed, parallel fibers arising from the ventral surface of the ceratohyal, and is broadly separated from the intermandibularis.

The shedding of the superficial larval mouthparts and the si-

TABLE 2.—Occurrence of Differentiation of the M. Intermandibularis in Anurans other than Hylids.

Numbers in Parentheses Indicate Species Examined by Trewavas (1933) and Included in the Total.

| Family | Genus | Differentiation | |
|-----------------|------------------------|--------------------------|-------------------------|
| | | Present (No. species) | Absent (No. species) |
| Ascaphidae | <i>Leiopelma</i> | 0 | 2 |
| Atelopodidae | <i>Brachycephalus</i> | 2(1) | 0 |
| Atelopodidae | <i>Dendrophryiscus</i> | 0 | 2(1) |
| Bufo | <i>Bufo</i> | 0 | 4(1) |
| Centrolenidae | <i>Centrolenella</i> | 0 | 3 |
| Dendrobatidae | <i>Calostethus</i> | 2 | 0 |
| Dendrobatidae | <i>Dendrobates</i> | 2 | 0 |
| Dendrobatidae | <i>Phyllobates</i> | 2 | 0 |
| Discoglossidae | <i>Bombina</i> | 0 | 2(1) |
| Leptodactylidae | <i>Crinia</i> | 0 | 8 |
| Leptodactylidae | <i>Cycloramphus</i> | 0 | 2 |
| Leptodactylidae | <i>Cyclorana</i> | 6 | 0 |
| Leptodactylidae | <i>Glauertia</i> | 0 | 2 |
| Leptodactylidae | <i>Heleioporus</i> | 0 | 5 |
| Leptodactylidae | <i>Lechriodus</i> | 0 | 2 |
| Leptodactylidae | <i>Leptodactylus</i> | 0 | 3(1) |
| Leptodactylidae | <i>Limnodynastes</i> | 0 | 7 |
| Leptodactylidae | <i>Mixophyes</i> | 0 | 2 |
| Leptodactylidae | <i>Neobatrachus</i> | 0 | 5 |
| Leptodactylidae | <i>Notaden</i> | 0 | 3 |
| Leptodactylidae | <i>Pseudophryne</i> | 0 | 3 |
| Leptodactylidae | <i>Taudactylus</i> | 0 | 2 |
| Leptodactylidae | <i>Uperoleia</i> | 0 | 2 |
| Microhylidae | <i>Asterophrys</i> | 4 | 0 |
| Microhylidae | <i>Breviceps</i> | 3(1) | 0 |
| Microhylidae | <i>Cophixalus</i> | 4 | 0 |
| Microhylidae | <i>Oreophryne</i> | 3(1) | 0 |
| Microhylidae | <i>Sphenophryne</i> | 6 | 0 |
| Ranidae | <i>Batrachylodes</i> | 2 | 0 |
| Ranidae | <i>Platymantis</i> | 6 | 0 |
| Ranidae | <i>Rana</i> | 0 | 12(6) |
| Ranidae | <i>Rhacophorus</i> | 0 | 3(2) |

multaneous commencement of development of the mandibles occurs after the emergence of the forelimbs and the commencement of absorption of the tail. There is no complete correlation between mandibular development and the alterations to external features used as reference points by Gosner (1960), so that figure 10b approximates to stages 42-43.

Loss of the mandibulolabialis and the appearance of the submentalis follow the initiation of development of the mandibles.

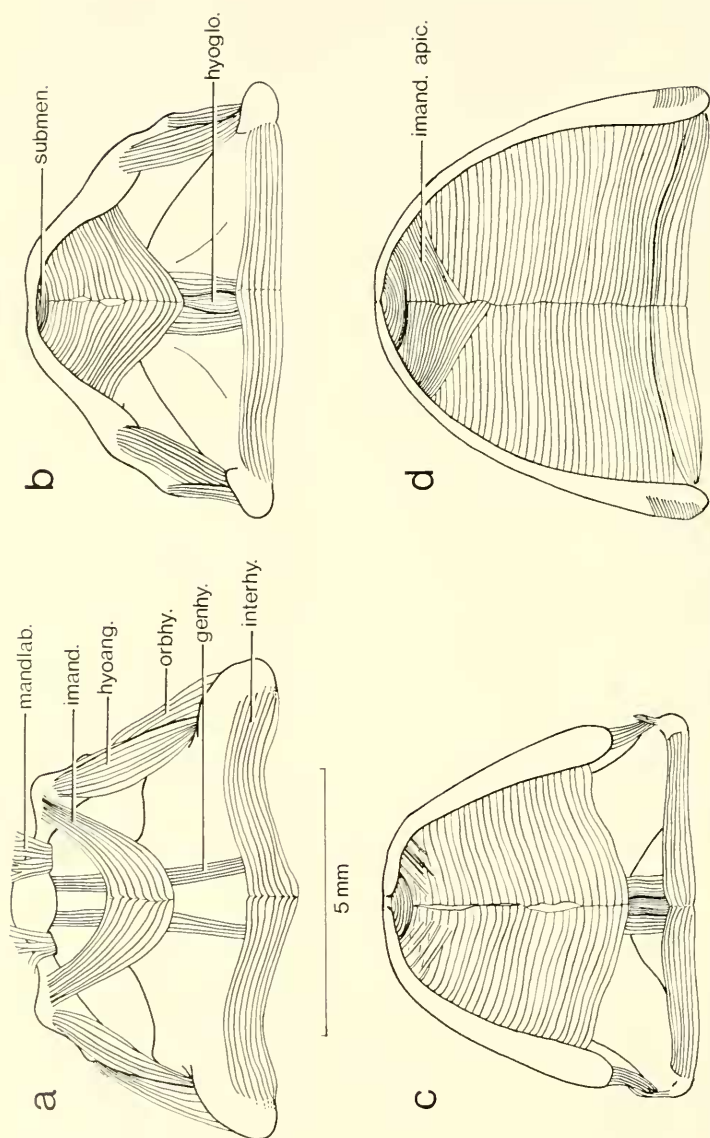


FIG. 10. Development of intermandibular musculature of *Hyla thesaurensis*: (a) Larval Stage 41; (b) Larval Stages 42-43; (c) Larval Stages 44-45; (d) Larval Stage 46. Abbreviations: *genhy.*, Musculus geniohyoideus; *hyoang.*, M. hyoangularis; *hyoglo.*, M. hyoglossus; *imand.*, principal element of M. intermandibularis; *imand. apic.*, apical element of M. intermandibularis; *interhy.*, M. interhyoideus; *mandlab.*, M. mandibulolabialis; *orbhy.*, M. orbitohyoideus; *submen.*, M. submental.

which elongate rapidly and rotate medially. The development of the intermandibularis accompanies the elongation of the mandible. Additional fibers arise anteriorly and posteriorly so that there is an increase in the number of fibers. Rotation transfers the site of attachment of the fibers of the intermandibularis from the ventral to the lateral surface of the mandible. No change was observed in the interhyoideus.

The final transition from tadpole to frog occurs through stages 44 to 45 by which time the habitus is that of a frog, but the larval tail is not completely absorbed, and persists as a small black stump. The mandibles have almost completed their development, and the extension of the intermandibularis has accompanied this development (Fig. 10c). The interhyoideus is not noticeably changed. Commencement of differentiation of the intermandibularis occurs at this ultimate point of metamorphic climax.

In material obtained in the field, stage 46 (Fig. 10d), marking the completion of metamorphosis and characterized by the lack of a tail stump, is understandably likely to be a heterogeneous group. It can include some individuals captured within hours of final absorption of the tail, and others perhaps several days after it. However, in the present material there is evidence to suggest genuine variation in the time elapsing before final development of the intermandibularis. In at least some individuals both the completion of apical differentiation of the intermandibularis, and the fusion of the customary sheet of this muscle with the anterior border of the interhyoideus are (in terms of external morphology), postmetamorphic. In the individual illustrated in figure 10d the apical element is incomplete on one side.

EVOLUTIONARY AND FUNCTIONAL SIGNIFICANCE OF SUPERFICIAL MANDIBULAR MUSCULATURE

Jarvik (1963) used the presence of supplementary elements of the intermandibularis, at least by inference, to support his hypothesis of the origin of the Anura from an osteolepiform fish stock. He also noted the resemblance of the anuran posterolateral element of the intermandibularis to the mammalian *M. digastricus* anterior. Jarvik cited the observations of Trewavas (1933) on differentiation of the anuran intermandibularis, and stressed the undoubted similarities in disposition between some of the supplementary elements of this muscle in the Anura and the submandibular dermal bones of osteolepiform fishes. From this and other data he concluded

that the various lines of osteolepiform stock are "characterised by a retrogressive development of the skeletal hard tissues."

Jarvik's interpretation involves the assumption that flat pinnate muscles are primitive features. In their functional analysis of muscle architecture, Gans and Bock (1965) provided no support for such a concept. They considered that some muscle systems may have undergone considerable structural change several times in the course of their evolution. It is also relevant to note that primitive anurans (*e.g.*, ascaphids), do not possess elements supplementary to the intermandibularis.

Intermandibular muscles are primarily involved in raising the floor of the mouth so that, from a functional viewpoint, transverse orientation of muscle fibers is an efficient arrangement. The employment of these same muscles in the anuran vocal sac structure introduces an additional function producing entirely different stresses at their sites of origin and insertion. Therefore it is reasonable to assume that this situation induces evolutionary change of the muscles.

From comparative morphology it is evident that the interhyoideus is the major component of the muscular wall surrounding the vocal sac. Thus the anterior and posterior development of the muscle, common to representatives of many genera, provides a means of increasing the length of the muscle fibers and presumably their ability to stretch.

In the case of the differentiated intermandibularis, post-metamorphic origin eliminates larval function; the direction of the fibers of the apical element (*e.g.*, in Australian *Hyla*) indicates that it evolved in response to posteriorly directed stress in the adult. This assumption is supported by reference to the musculature of *Rhinoderma darwini*, a species in which the vocal sac also functions as a brood pouch and extends further posteriorly than in any other anuran.

Beddard (1903) drew attention to the presence of a triangular muscle at the apex of the mandibles of *R. darwini*. Uncertain of its identity, he suggested that it might represent the genioglossus. Trewavas (1933) identified the muscle as the intermandibularis, which in that species apparently has differentiated to the ultimate point of forming an entirely separate muscle block, not an element lying ventral to the principal muscle. The presence of tadpoles in the vocal sac would exert stress directed posteriorly. Therefore, I suggest that differentiation of the intermandibularis into separate elements is a specialization evolving within the Anura.

The similarity between the supplementary lateral elements and the mammalian digastricus anterior suggested by Jarvik (1963), is confined to their shape and site of origin. There is no evidence of homology.

It is possible to detect at least four diverging lines in the evolution of the vocal sac and associated musculature in which the intermandibularis is not differentiated: (1) the median submandibular or substernal site involving both the intermandibularis and interhyoideus, although the interhyoideus is the major component. This structure is common to most species now referred to *Hyla*; (2) involvement solely of the interhyoideus as in *Tripurion spatulatus*; (3) development of a bilobular substernal structure (e.g., *Smilisca*); and (4) a bilobular supramandibular structure in *Phrynohyas*, *Trachycephalus* and *Osteocephalus*.

Blair (1964) considered that paired vocal sacs represent the primitive condition and that single submandibular sacs are derived because they pass through a transitory bilobular stage in the course of their ontogeny in *Bufo regularis* (Inger and Greenberg, 1956), and pairing occurs in the Pelobatidae (McAllister, 1959). However, in hylids other than *H. infrafrenata*, the evolution of separate bilobular structures involves change in development of various groups of muscle fibers; these changes are accompanied by alterations to the sites of muscle attachment. In contrast, the submandibular site involves scant modification of the basic anuran musculature. In the case of *H. infrafrenata*, the bilobular form is clearly a consequence of episternal intrusion. Therefore, I am of the opinion that hylid bilobular vocal sacs are not primitive structures.

It has been suggested that in the Ranidae the evolution of lateral outgrowths of the vocal sac is a consequence of the presence of the musculus cutaneous pectoris, which limits the extent to which the submandibular site can be distended (Tyler, 1970). This muscle does not occur in the Hylidae, and I have been unable to find structural features likely to contribute to the evolution of supramandibular vocal sacs in certain genera. Detailed knowledge of the sites selected for calling by the males may indicate a situation in which their possession would be advantageous.

Conceivably the very highly specialized vocal sacs of *Phrynohyas* and *Trachycephalus* could have been derived from the simpler structures now found in some species of *Osteocephalus*. However, there is no evidence that any supramandibular sacs evolved from substernal structures; it is more likely that each (substernal and supramandibular) evolved independently.

PHYLOGENETIC IMPLICATIONS OF SUPERFICIAL MANDIBULAR
MUSCULATURE

Genera that can be demonstrated to share a close phylogenetic relationship using other morphological or biological criteria, exhibit similar mandibular musculature, and the musculature does not provide a means of distinguishing such genera. Thus, superficial mandibular musculature is here regarded a conservative feature, and particular attention is devoted to those genera sharing similar derived states involving differentiation of the intermandibularis.

Duellman (1968) considered that *Agalychnis*, *Pachymedusa* and *Phyllomedusa* exhibit such a distinctive combination of characteristics that they merit recognition as a subfamily (the Phyllomedusinae). The form of posterolateral differentiation of the intermandibularis shared by these three genera is quite unlike that of other hylid genera and lends support to Duellman's proposal. Several authors had previously commented on the close, superficial morphological resemblance of *Nyctimystes* to the phyllomedusines. Although the intermandibularis of *Nyctimystes* is differentiated, the form and position of the supplementary element is unlike that of the phyllomedusines, and identical to that characterizing Australian *Hyla*. This indicates that *Nyctimystes* is not closely related to the phyllomedusines; superficial similarities in features such as the shape of the constricted pupil are the result of convergence. It also indicates that *Nyctimystes* and Australian *Hyla* are derived from a single ancestral stock.

The familial disposition of *Allophryne* has been the subject of debate, and Lynch and Freeman (1966) tentatively placed it in the Hyliidae because they found that it differed less from the members of that family than from those of any other. That the nature of the differentiation of the intermandibularis of *Allophryne* is unique in the Hyliidae is not surprising. In the absence of a comprehensive survey of anuran genera the distribution of all such different forms of differentiation is unknown; of those reported here the only ones exhibiting supplementary anterolateral elements similar to those of *Allophryne* are the dendrobatids *Colostethus*, *Dendrobates*, and *Phyllobates*.

As a background to an interpretation of the morphological divergence in *Hyla*, it should be noted that the inclusion of Australo-Papuan species in *Hyla* is a consequence of a series of assumptions made by early workers. Externally a tree-frog is a tree-frog. In fact, there is such marked convergence between arboreal hyliids and ranids that two Papuan hyliids were originally referred to the ranid

(hyperoliid) genus *Hyperolius*, whereas the ranid (rhacophorid) *Rhacophorus wirzi* was originally described as a *Hyla*. Daudin (1802) was probably the first author to refer an Australian species to the genus *Hyla*; subsequently the action has never been questioned seriously. Since then, numerous genera proposed for Australian species and based on external features have been progressively suppressed in favor of the all-embracing *Hyla*, although there have been no morphological comparisons of adequate numbers of species from different geographic regions to enable any critical conclusions.

On the basis of the data presented here I conclude that it is not possible to include species with differentiated and other lacking differentiated muscles in a single genus. *Hyla* as presently constituted contains three distinct morphological groups; there is a complete correlation between these morphological groups and their geographical distributions. The retention of the Australo-Papuan species in *Hyla* cannot be justified. Also I conclude that the divergence of the West Indian species of the *septrionalis* group merits their removal from *Hyla*. Dr. Trueb is currently examining the cranial osteology of these and possibly phylogenetically related frogs; a joint publication is anticipated.

TAXONOMIC PROPOSALS

I propose that the generic name *Litoria* Tschudi (1838) be used for all Australo-Papuan species currently referred to *Hyla* (Table 3). *Litoria* is characterized by a differentiated musculus intermandibularis. The supplementary element of the intermandibularis is completely separate from the principal body of the muscle and lies at the apex of the mandibles on each side of, and adjacent to, the musculus submental.

The resurrection of *Litoria* for the Australo-Papuan species results in the restriction of *Hyla* to species occurring in the Nearctic, Palearctic, Oriental and Neotropical regions. The intermandibularis of *Hyla* is not differentiated and remains a simple muscle, the fibers of which lie in a single plane. Such a definition excludes the West Indian *Hyla septrionalis* group, which differ from the remainder of the genus, and from *Litoria*, in exhibiting partial differentiation of the intermandibularis. These same species have a dermal sphenethmoid (Trueb, 1966). The diagnosis of *Hyla* formerly has been modified accordingly to accommodate them (Goin, 1961). The continued retention of this group of species in *Hyla* is a temporary measure and my definition of the condition of the intermandibularis in *Hyla* is based on this consideration.

TABLE 3.—Alphabetical Synonymy of the Hyloid Genus *Litoria*

| Trivial name, original nomenclatural combination, author and date | Present name |
|---|----------------------------------|
| <i>adelaidensis</i> (<i>Hyla</i>) Gray, 1841 | <i>adelaidensis</i> |
| <i>affinis</i> (<i>Pelodytes</i>) Gray, 1842 | <i>latopalmata</i> |
| <i>albolabris</i> (<i>Hyla</i>) Wandolleck, 1911 | <i>albolabris</i> |
| <i>alpina</i> (<i>Hyla ewingi</i>) Fry, 1915 | <i>ewingi</i> |
| <i>amboinensis</i> (<i>Hyla</i>) Horst, 1883 | <i>amboinensis</i> |
| <i>angiana</i> (<i>Hyla</i>) Boulenger, 1915 | <i>angiana</i> |
| <i>angularis</i> (<i>Hyla</i>) Loveridge, 1945 | <i>angiana</i> |
| <i>arfakiana</i> (<i>Hyla</i> (<i>Litoria</i>)) Peters & Doria, 1878 | <i>arfakiana</i> |
| <i>aruensis</i> (<i>Hyla</i>) Horst, 1883 | <i>aruensis</i> |
| <i>atropunctata</i> (<i>Hyla</i>) Van Kampen, 1923 | <i>nigropunctata</i> |
| <i>aurea</i> (<i>Rana</i>) Lesson, 1830 | <i>aurea aurea</i> |
| <i>austriasiae</i> (<i>Rana</i>) Schneider, 1799 | <i>caerulea</i> |
| <i>barringtonensis</i> (<i>Hyla phyllochroa</i>) Copland, 1957 | <i>phyllochroa</i> |
| <i>becki</i> (<i>Hyla</i>) Loveridge, 1945 | <i>becki</i> |
| <i>bersteini</i> (<i>Hyla</i>) Horst, 1883 | <i>nigropunctata</i> |
| <i>bicolor</i> (<i>Eucnemis</i>) Gray, 1842 | <i>bicolor</i> |
| <i>binoculata</i> (<i>Hyla</i>) Gray, 1841 | <i>adelaidensis</i> |
| <i>blandsuttoni</i> (<i>Hyla</i>) Proctor, 1924 | ? <i>aurea</i> |
| <i>booroolongensis</i> (<i>Hyla</i>) Moore, 1961 | <i>booroolongensis</i> |
| <i>boulengeri</i> (<i>Hylella</i>) Méhely, 1897 | <i>pygmaea</i> |
| <i>brongersmai</i> (<i>Hyla</i>) Loveridge, 1945 | <i>brongersmai</i> |
| <i>bulmeri</i> (<i>Hyla</i>) Tyler, 1968 | <i>bulmeri</i> |
| <i>burrowsi</i> (<i>Hyla</i>) Scott, 1942 | <i>burrowsi</i> |
| <i>caerulea</i> (<i>Rana</i>) White, 1790 | <i>caerulea</i> |
| <i>calliscelis</i> (<i>Hyla</i>) Peters, 1875 | <i>ewingi</i> |
| <i>capitula</i> (<i>Hyla</i>) Tyler, 1968 | <i>capitula</i> |
| <i>castanea</i> (<i>Hyla</i>) Steindachner, 1867 | ? <i>aurea raniformis</i> |
| <i>chloris</i> (<i>Hyla</i>) Boulenger, 1893 | <i>chloris</i> |
| <i>chloronota</i> (<i>Hyla</i>) Boulenger, 1911 | <i>chloronota</i> |
| <i>citropa</i> (<i>Dendrokyas</i>) Tschudi, 1838 | <i>citropa</i> |
| <i>congenita</i> (<i>Hyla</i> (<i>Litoria</i>)) Peters & Doria, 1878 | <i>congenita</i> |
| <i>contrastens</i> (<i>Hyla</i>) Tyler, 1968 | <i>contrastens</i> |
| <i>copei</i> (<i>Litoria</i>) Steindachner, 1867 | ? <i>lesueuri</i> |
| <i>coplandi</i> (<i>Hyla</i>) Tyler, 1968 | <i>coplandi</i> |
| <i>cyanca</i> (<i>Hyla</i>) Daudin, 1802 | <i>caerulea</i> |
| <i>cyclorhynchus</i> (<i>Hyla aurea</i>) Boulenger, 1882 | <i>cyclorhynchus</i> |
| <i>darlingtoni</i> (<i>Hyla</i>) Loveridge, 1945 | <i>darlingtoni</i> |
| <i>dayi</i> (<i>Hyla</i>) Gunther, 1897 | <i>dayi</i> |
| <i>dentata</i> (<i>Hyla</i>) Keferstein, 1868 | <i>dentata</i> |
| <i>dimolops</i> (<i>Hyla</i>) Cope, 1869 | <i>cyclorhynchus</i> |
| <i>dolichopsis</i> (<i>Calamita</i>) Cope, 1867 | <i>infrafrenata infrafrenata</i> |
| <i>dorsalis</i> (<i>Litoria</i>) Mackay, 1878 | <i>dorsalis</i> |
| <i>dorsivena</i> (<i>Hyla</i>) Tyler, 1968 | <i>dorsivena</i> |
| <i>elegans</i> (<i>Fanchonia</i>) Werner, 1893 | <i>aurea aurea</i> |
| <i>eucnemis</i> (<i>Hyla</i>) Lönnberg, 1900 | <i>eucnemis</i> |
| <i>everetti</i> (<i>Hyla</i>) Boulenger, 1897 | <i>everetti</i> |

TABLE 3.—*Continued*

| Trivial name, original nomenclatural combination, author and date | Present name |
|--|----------------------------------|
| <i>ewingii</i> (<i>Hyla</i>) Duméril & Bibron, 1841 | <i>ewingi</i> |
| <i>fallax</i> (<i>Hyla</i>) Boulenger, 1898 | <i>pygmaca</i> |
| <i>flavomaculata</i> (<i>Nyctimystes</i>) Forcart, 1953 | <i>darlingtoni</i> |
| <i>flavoviridis</i> (<i>Ranoidea</i>) Girard, 1853 | <i>lesueuri</i> |
| <i>fordii</i> (<i>Hyla</i>) Gunther, 1876 | <i>gracilentia</i> |
| <i>freycineti</i> (<i>Litoria</i>) Tschudi, 1838 | <i>freycineti</i> |
| <i>genimaculata</i> (<i>Hyla</i>) Horst, 1883 | <i>genimaculata</i> |
| <i>gilleni</i> (<i>Hyla</i>) Spencer, 1896 | <i>caerulea</i> |
| <i>glauerti</i> (<i>Hyla bicolor</i>) Copland, 1957 | <i>glauerti</i> |
| <i>gracilentia</i> (<i>Hyla</i>) Peters, 1869 | <i>gracilentia</i> |
| <i>graminea</i> (<i>Hyla</i>) Boulenger, 1905 | <i>graminea</i> |
| <i>granulata</i> (<i>Pelodytes</i>) Peters, 1873 | <i>gracilentia</i> |
| <i>guttata</i> (<i>Litoria</i>) Macleay, 1877 | <i>infrafrenata infrafrenata</i> |
| <i>impura</i> (<i>Hyla</i> (<i>Litoria</i>)) Peters & Doria, 1878 | <i>thesaurensis</i> |
| <i>inermis</i> (<i>Chiroleptes</i>) Peters, 1867 | <i>inermis</i> |
| <i>infrafrenata</i> (<i>Hyla</i>) Gunther, 1867 | <i>infrafrenata infrafrenata</i> |
| <i>inguinalis</i> (<i>Hyla</i>) Ahl, 1935 | <i>ewingi</i> |
| <i>iris</i> (<i>Hyla</i>) Tyler, 1962 | <i>iris</i> |
| <i>irrorata</i> (<i>Hyla</i>) de Vis, 1884 | <i>irrorata</i> |
| <i>iuxtaewingii</i> (<i>Hyla ewingi</i>) Copland, 1957 | <i>ewingi</i> |
| <i>jacksoniensis</i> (<i>Ranoides</i>) Tschudi, 1838 | <i>aurea aurea</i> |
| <i>jenolanensis</i> (<i>Hyla</i>) Copland, 1957 | <i>jenolanensis</i> |
| <i>jervisiensis</i> (<i>Hyla</i>) Duméril & Bibron, 1841 | <i>jervisiensis</i> |
| <i>jeudii</i> (<i>Hyla</i>) Werner, 1901 | <i>jeudei</i> |
| <i>kampeni</i> (<i>Hyla</i>) Barbour, 1908 | <i>amboinensis</i> |
| <i>kinghorni</i> (<i>Hyla</i>) Loveridge, 1950 | <i>kinghorni</i> |
| <i>latopalmata</i> (<i>Litoria</i>) Gunther, 1867 | <i>latopalmata</i> |
| <i>lessoni</i> (<i>Euscelis</i>) Fitzinger, 1861 | <i>lesueuri</i> |
| <i>lesueuri</i> (<i>Hyla</i>) Duméril & Bibron, 1841 | <i>lesueuri</i> |
| <i>leucova</i> (<i>Hyla</i>) Tyler, 1968 | <i>leucova</i> |
| <i>longicrus</i> (<i>Hylella</i>) Boulenger, 1911 | <i>longicrus</i> |
| <i>louisadensis</i> (<i>Hyla</i>) Tyler, 1968 | <i>louisadensis</i> |
| <i>loveridgei</i> (<i>Hyla ewingi</i>) Copland, 1957 | <i>ewingi</i> |
| <i>loveridgei</i> (<i>Nyctimystes</i>) Neill, 1954 | <i>genimaculata</i> |
| <i>lutea</i> (<i>Hyla</i>) Boulenger, 1887 | <i>lutea</i> |
| <i>luteiventris</i> (<i>Hyla</i>) Ogilby, 1907 | <i>gracilentia</i> |
| <i>macgregori</i> (<i>Hyla</i>) Ogilby, 1890 | <i>congenita</i> |
| <i>macrops</i> (<i>Hyla</i>) Boulenger, 1883 | <i>thesaurensis</i> |
| <i>maculata</i> (<i>Hyla</i>) Spencer, 1901 | <i>maculata</i> |
| <i>major</i> (<i>Hyla aurea</i>) Copland, 1957 | ? <i>aurea raniformis</i> |
| <i>marmorata</i> (<i>Litoria</i>) Duméril, 1853 | <i>cyclorhynchus</i> |
| <i>mehelji</i> (<i>Hyla</i>) Nieden, 1923 | <i>pygmaca</i> |
| <i>meiriana</i> (<i>Hyla</i>) Tyler, 1969 | <i>meiriana</i> |
| <i>microbelos</i> (<i>Hyla dorsalis</i>) Cogger, 1966 | <i>microbelos</i> |
| <i>micromembrana</i> (<i>Hyla</i>) Tyler, 1963 | <i>micromembrana</i> |

TABLE 3.—Continued

| Trivial name, original nomenclatural combination, author and date | Present name |
|---|----------------------------------|
| <i>militarius</i> (<i>Pelodryas</i>) Ramsay, 1878 | <i>infrafrenata militaria</i> |
| <i>milneana</i> (<i>Nyctimystes</i>) Loveridge, 1945 | <i>thesaurensis</i> |
| <i>minima</i> (<i>Hyla</i>) Tyler, 1962 | <i>angiana</i> |
| <i>modica</i> (<i>Hyla</i>) Tyler, 1968 | <i>modica</i> |
| <i>moorei</i> (<i>Hyla</i>) Copland, 1957 | <i>moorei</i> |
| <i>multiplica</i> (<i>Hyla</i>) Tyler, 1964 | <i>multiplica</i> |
| <i>mystacina</i> (<i>Hyla</i> (<i>Litoria</i> ?)) Keferstein, 1867 | ? <i>freycineti</i> |
| <i>mystax</i> (<i>Hyla</i>) Van Kampen, 1906 | <i>mystax</i> |
| <i>nannotis</i> (<i>Hyla</i>) Andersson, 1916 | <i>nannotis</i> |
| <i>napaea</i> (<i>Hyla</i>) Tyler, 1968 | <i>napaea</i> |
| <i>nasutus</i> (<i>Pelodytes</i>) Gray, 1841 | <i>nasuta</i> |
| <i>nigrofrenata</i> (<i>Hyla</i>) Gunther, 1867 | <i>nigrofrenata</i> |
| <i>nigropunctatus</i> (<i>Hyperolius</i>) Meyer, 1874 | <i>nigropunctata</i> |
| <i>nudidigitus</i> (<i>Hyla phyllochroa</i>) Copland, 1962 | <i>phyllochroa</i> |
| <i>oberonensis</i> (<i>Hyla ewingii</i>) Copland, 1957 | <i>ewingi</i> |
| <i>obtusirostris</i> (<i>Litoria</i>) Meyer, 1875 | <i>obtusirostris</i> |
| <i>orientalis</i> (<i>Hyla ewingii</i>) Fletcher, 1898 | <i>ewingi</i> |
| <i>ouwensii</i> (<i>Hyla</i>) Barbour, 1908 | <i>nigropunctata</i> |
| <i>papua</i> (<i>Hyla</i>) Van Kampen, 1909 | <i>genimaculata</i> |
| <i>papuensis</i> (<i>Hyla</i>) Werner, 1901 | <i>amboinensis</i> |
| <i>parvidens</i> (<i>Hyla</i>) Peters, 1875 | <i>ewingi</i> |
| <i>pearsoni</i> (<i>Hyla</i>) Copland, 1960 | <i>pearsoni</i> |
| <i>pearsoniana</i> (<i>Hyla</i>) Copland, 1961 | <i>pearsoni</i> |
| <i>peninsulae</i> (<i>Hyla</i>) de Vis, 1884 | <i>nasuta</i> |
| <i>peronii</i> (<i>Dendrohyas</i>) Tschudi, 1838 | <i>peroni</i> |
| <i>phyllochroa</i> (<i>Hyla</i>) Gunther, 1863 | <i>phyllochroa</i> |
| <i>pollicaris</i> (<i>Hyla dolichopsis</i>) Werner, 1898 | <i>infrafrenata militaria</i> |
| <i>pratti</i> (<i>Hyla</i>) Boulenger, 1911 | <i>pratti</i> |
| <i>prora</i> (<i>Hyla</i>) Menzies, 1969 | <i>prora</i> |
| <i>punctata</i> (<i>Litoria</i>) Duméril, 1853 | <i>cyclorhynchus</i> |
| <i>pygmaeus</i> (<i>Hyperolius</i>) Meyer, 1874 | <i>pygmaea</i> |
| <i>raniformis</i> (<i>Chirodryas</i>) Keferstein, 1867 | <i>aurea raniformis</i> |
| <i>resplendens</i> (<i>Ranoidea</i>) Girard, 1853 | <i>aurea aurea</i> |
| <i>rhacophorus</i> (<i>Hyla</i>) Van Kampen, 1909 | <i>eucnemis</i> |
| <i>rothii</i> (<i>Hyla</i>) de Vis, 1884 | <i>rothi</i> |
| <i>rubella</i> (<i>Hyla</i>) Gray, 1842 | <i>rubella</i> |
| <i>sanguinolenta</i> (<i>Hyla</i>) Van Kampen, 1909 | <i>sanguinolenta</i> |
| <i>schuetti</i> (<i>Hyla</i>) Keferstein, 1868 | <i>adelaidensis</i> |
| <i>semoni</i> (<i>Hyla</i>) Boettger, 1894 | <i>nasuta</i> |
| <i>serrata</i> (<i>Hyla</i>) Andersson, 1916 | <i>eucnemis</i> |
| <i>solomonis</i> (<i>Hyla</i>) Vogt, 1912 | <i>thesaurensis</i> |
| <i>spaldingi</i> (<i>Hyla</i>) Hosmer, 1964 | <i>wotjulumensis</i> |
| <i>spengeli</i> (<i>Hyla</i>) Boulenger, 1912 | <i>infrafrenata infrafrenata</i> |
| <i>spinifera</i> (<i>Hyla</i>) Tyler, 1968 | <i>spinifera</i> |
| <i>tenuigranulata</i> (<i>Hyla dolichopsis</i>) Boettger, 1895 | <i>infrafrenata infrafrenata</i> |

TABLE 3.—*Concluded*

| Trivial name, original nomenclatural combination, author and date | Present name |
|---|----------------------------------|
| <i>thesaurensis</i> (<i>Hyla</i>) Peters, 1878 | <i>thesaurensis</i> |
| <i>thyposticta</i> (<i>Hyla</i>) Cope, 1869 | <i>cyclorhynchus</i> |
| <i>toruieri</i> (<i>Hyla</i>) Nieden, 1923 | <i>latopalmata</i> |
| <i>trinilensis</i> (<i>Hyla</i>) Ahl, 1929 | <i>infrafrenata infrafrenata</i> |
| <i>ulongae</i> (<i>Hyla aurea</i>) Copland, 1957 | <i>aurea aurea</i> |
| <i>unicolor</i> (<i>Hyla</i> (<i>Litoria</i>) <i>freycineti</i>) Keferstein, 1867 | <i>freycinetti</i> |
| <i>vagabunda</i> (<i>Hyla</i> (<i>Litoria</i>)) Peters & Doria, 1878 | <i>vagabunda</i> |
| <i>verreauxii</i> (<i>Hyla</i>) Duméril, 1853 | <i>verreauxi</i> |
| <i>verruculata</i> (<i>Hyla</i> (<i>Litoria</i>) <i>freycineti</i>) Keferstein, 1867 | <i>freycinetti</i> |
| <i>vinosa</i> (<i>Hyla</i>) Lamb, 1911 | ? <i>vinosa</i> |
| <i>wilcoxi</i> (<i>Litoria</i>) Gunther, 1864 | <i>lesueuri</i> |
| <i>wisselensis</i> (<i>Hyla</i>) Tyler, 1968 | <i>wisselensis</i> |
| <i>wollastoni</i> (<i>Hyla</i>) Boulenger, 1914 | <i>arfakiana</i> |
| <i>watjulumensis</i> (<i>Hyla latopalmata</i>) Copland, 1957 | <i>wotjulumensis</i> |

ACKNOWLEDGMENTS

The studies reported here were undertaken principally at the South Australian Museum and completed at the University of Kansas Museum of Natural History. Grateful acknowledgment is made to the Executive of the Commonwealth Scientific and Industrial Research Organisation for providing a grant from the Science and Industry Endowment Fund enabling me to visit the University of Kansas. I am greatly indebted to Dr. W. E. Duellman and Dr. L. Trueb for the generous hospitality extended to me, and for the provision of research facilities. In addition they constructively criticized the manuscript and Dr. Trueb gave expert advice and assistance in the preparation of illustrations.

For the loan, exchange or donation of specimens I thank Dr. W. Auffenberg (Florida State Museum), Dr. J. Eiselt (Naturhistorische Museum, Vienna), Dr. J. Hickman (University of Tasmania), Dr. R. F. Inger (Field Museum of Natural History), Dr. A. E. Leviton (California Academy of Sciences), Dr. J. A. Peters (United States National Museum), Dr. P. E. Vanzolini (Departamento de Zoologia, Sao Paulo, Brazil) and Dr. E. E. Williams (Museum of Comparative Zoology).

I would also like to express my thanks to Dr. W. G. Inglis and the late Mr. F. J. Mitchell (South Australian Museum), who discussed various aspects of the studies with me and were a source of encouragement; Dr. A. A. Martin and Mr. G. Watson (University of Melbourne), who provided unpublished data on larval mor-

phology; Miss T. Mannik, who prepared histological material; and Miss C. Pulley for laboratory assistance.

SUMMARY

Hyliid frogs vary in superficial mandibular musculature and in vocal sac structure. In several genera the *Musculus intermandibularis* is differentiated by the development of supplementary elements lying ventral to the principal element of the muscle; the *M. interhyoideus* develops in various ways in association with the vocal sac. Of 31 hyliid genera and 57 genera representing nine other families, *Hyla* was found to be the only genus containing some species that possess supplementary elements and some species that lack them.

Studies on muscle ontogeny revealed that the supplementary elements originate at metamorphic climax. The process of differentiation is considered to have evolved within the Anura in response to stress resulting from the evolution of the vocal sac. Genera that can be demonstrated to be phylogenetically closely related by other criteria share similar superficial mandibular musculature (e.g., Phyllomedusinae). Such musculature is therefore considered to be conservative. Accordingly it is not possible to retain in a single genus some species with supplementary elements to the intermandibularis and other species lacking them.

In *Hyla* there is a correlation between the form of mandibular musculature and the geographic distribution of the species. All Australian species share one morphological form unique to that region; the West Indies species of the *Hyla septentrionalis* group are the only other species of *Hyla* with differentiated muscles.

The resurrection of *Litoria* Tschudi is proposed to accommodate all Australian species currently referred to *Hyla*. The *Hyla septentrionalis* group is the subject of separate study. The genus *Hyla* is redefined.

APPENDIX

List of hyliid genera, species and subspecies examined

(1) signifies that larvae as well as adults were examined

Australian Region

Litoria adalaidensis, *L. amboinensis*, *L. angiana*, *L. arfakiana*, *L. aurea* (1), *L. bicolor*, *L. booroolongensis*, *L. burrowsi*, *L. caerulea*, *L. congenita*, *L. contrastens*, *L. coplandi*, *L. cyclorhynchus*, *L. darlingtoni*, *L. dayi*, *L. dentata*, *L. dorsalis*, *L. dorsivena*, *L. eucnemis*, *L. everetti*, *L. ewingi* (1), *L. genimaculata*, *L. glauerti*, *L. gracilentia*, *L. i. infrafronata*, *L. infrafronata militaria*, *L. iris*, *L. latopalmata*, *L. lesueuri*, *L. longirus*, *L. lutea*, *L. microbelos*, *L. micromembrana*, *L. modica*, *L. moorci*, *L. multiplica*, *L. namotis*, *L. nasuta*, *L. nigrofrenata*, *L. nigropunctata*, *L. peroni*, *L. phyllochroa*, *L. pygmaca*, *L. rothi*, *L. rubella*, *L. sanguinolenta*, *L. spinifera*, *L. thesaurensis*

(1), *L. wisselensis* (1), *L. wotjulumensis*; *Nyctimystes cheesmanae*, *N. daymani*, *N. foricula*, *N. kuhori*, *N. narinosa*, *N. papua*, *N. pulchra*, *N. tympanocryptis*, *N. zueciferi*.

Nearctic Region

Acris crepitans, *A. gryllus*.

Hyla crucifer, *H. femoralis*, *H. gratiosa*, *H. regilla*, *H. squirella*, *H. versicolor*.

Limnaeodius ocularis.

Pseudacris nigrita, *P. ornata*, *P. triseriata*.

Palearctic Region

Hyla a. arborea, *H. arborea cretensis*.

Oriental Region

Hyla arborea japonica, *H. simplex*.

Neotropical Region

Agalychnis callidryas, *A. saltator*.

Allophryne ruthveni.

Amphignathodon guntheri.

Anotheca spinosa.

Aparasphenodon brunoii.

Aplastodiscus perviridis.

Argenteohyla siemersi.

Corythomantis greeni.

Cryptobatrachus fulurmanni.

Flectonotus fissilis.

Fritziana goeldi, *F. ohausi*.

Gastrotheca ceratophrys, *G.m. marsupiatum*, *G. uicefori*.

Hemiphractus proboscideus, *H. scutatus*.

Hyla albobrunnea, *H. albobrunnea*, *H. albobrunnea*, *H. albobrunnea*, *H. albosignata*, *H. bifurca*, *H. bipunctata*, *H. boans*, *H. boulengeri*, *H. brieni*, *H. brunnea*, *H. calcarata*, *H. catharinae*, *H. circumdata*, *H. columbiana*, *H. colymba*, *H. crepitans*, *H. crosopodospila*, *H. cuspidata*, *H. decipiens*, *H. depressiceps*, *H. dominicensis*, *H. ebracatta*, *H. egleri*, *H. elongata*, *H. euphorbiacea*, *H. faber*, *H. fasciata*, *H. fuscomarginata*, *H. fuscovaria*, *H. garbei*, *H. geographica*, *H. gougei*, *H. granosa*, *H. granulata*, *H. hayi*, *H. heilprini*, *H. lancasteri*, *H. lanciformis*, *H. leucophyllata*, *H. lichenata*, *H. lindneri*, *H. loquax*, *H. marianae*, *H. marmorata*, *H. megapodia*, *H. microcephala*, *H. microps*, *H. miliaris*, *H. minuta*, *H. misera*, *H. nana*, *H. nasica*, *H. pardalis*, *H. parviceps*, *H. pellucens*, *H. pentheter*, *H. phrynodermis*, *H. pickeli*, *H. polytaenia*, *H. pulchella*, *H. prasina*, *H. pulchellilineata*, *H. punctata*, *H. raddiana*, *H. reticulata*, *H. ricularis*, *H. robertsoni*, *H. rondoniae*, *H. rosenbergi*, *H. rubra*, *H. sanborni*, *H. senicula*, *H. septentrionalis*, *H. smaragdina*, *H. spegazzini*, *H. subocularis*, *H. truncata*, *H. vasta*, *H. werneri*, *H. wilderi*.

Nyctimantis rugiceps.

Osteocephalus buckleyi, *O. lepreurii*, *O. pearsoni*, *O. taurinus*, *O. verrucigerus*.

Pachymedusa dacnicolor.

Phrynobates coriacea, *P. mesophaea*, *P. venulosa*.

Phyllodytes wuchereri.

Phyllomedusa appendiculata, *P. bicolor*, *P. burmeisteri bahiana*, *P.b. burmeisteri*, *P. burmeisteri ilheringi*, *P. edentula*, *P. fimbriata*, *P. guttata*, *P.*

- hypochondrialis*, *P. lemur*, *P. rohdei*.
Plectrohyla guatamalensis, *P. ixil*.
Pternohyla fodiens.
Ptychohyla leonhardschultzei, *P. spinipollex*.
Smilisca baudini, *S. phacota*, *S. puma*.
Sphacnorrhynchus aurantiacus, *S. eurhostus*, *S.o. orophilus*.
Trachycephalus jordani, *T. nigromaculatus*.
Triprion petasatus, *T.s. spatulus*.

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